

## Food composition of three *Rana* species in Kis-Balaton Nature Reserve

By

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**Abstract.** Diet composition of *Rana esculenta* (47 specimens), *R. arvalis* (23) and *R. dalmatina* (6) were studied in the Kis-Balaton Nature Reserve during the autumn of 1984. Based on stomach analysis the most frequent prey groups were Curculionidae, Carabidae, Araneidae, Formicidae, Mollusca and Heteroptera. All the three species showed opportunism while foraging on ground and small plants. There was no remarkable difference in the diet composition of frogs between dry and wet habitats. In addition data of 158 specimens of the three frog species found in I. SZABÓ's collection were also analysed.

Only few publications have been appeared on the species composition, population dynamics and reproduction of Hungarian anuran populations (DELY, 1954, 1964 a, b, 1967; ILOSVAY, 1980). Although frogs play important roles as secondary or tertiary predators in communities along riversides or other wet habitats, only few data were published on their food composition in Hungary (RAINISS, 1957; MOLNÁR, 1967).

The aim of this paper is to describe the diet composition of three frog species (*Rana esculenta* complex, *R. arvalis* and *R. dalmatina*) in the Kis-Balaton Nature Reserve. There are two reasons which give a special importance to this reserve area. On the one hand this is the oldest protected Hungarian nature reserve as it has been designated in 1951. On the other hand this area will be destroyed in the near future to build a large artificial water reservoir. As a part of a large survey project aiming to monitor the present status of this area we investigated the habitat preference and food selection of anuran species in the nature reserve area and its surroundings. In this paper we present data on the diet composition of the three dominant *Rana* species collected in 1984. In addition we analysed the data of the three frog species collected by Dr. I. SZABÓ from 1956 to 1961 at different parts of Hungary.

### Methods

We collected 76 specimens of the three frog species (47 *esculenta*, 23 *arvalis*, 6 *dalmatina*) altogether. Frogs were killed by chlorophorm. We measured the snout-vent length (SVL) with ruler and body mass with Pesola spring balance. After sexing, the stomachs were removed and food items were sorted and measured to 1.0 mm under binocular microscope. Prey specimens were stored in alcohol until determination.

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Table 1. Food composition (based on prey items) of three anuran species at wet (W) and dry (D) habitats of Kis-Balaton in 1984

Prey taxa	Anuran species								
	<i>R. esculenta</i>			<i>R. arvalis</i>			<i>R. dalmatina</i>		
	W	D	Total	W	D	Total	W	D	Total
Animal food									
Annelida	1	—	1	—	1	1	—	—	—
Mollusca	15	1	16	7	6	13	5	3	8
Isopoda	9	—	9	5	1	6	8	—	8
Amphipoda									
<i>Gammarus</i> spp.	2	—	2	1	—	1	1	—	1
Diplopoda									
Polidesmidae	—	—	—	3	1	4	—	—	—
Julidae	1	—	1	1	5	6	—	—	—
Chilopoda	3	1	4	1	4	5	—	—	—
Collembola	1	—	1	—	—	—	—	—	—
Odonata	—	—	—	—	1	1	—	—	—
Orthoptera									
Arctiidae	3	—	3	—	—	—	—	—	—
Tettigoniidae	—	—	—	1	—	1	—	—	—
Mantidea	—	—	—	—	2	2	—	—	—
Psocoptera	—	—	—	1	—	1	—	—	—
Heteroptera	2	1	3	1	2	3	4	3	7
Homoptera									
Aphididae	4	—	4	—	—	—	5	—	5
Homoptera indet.	29	4	33	2	6	8	—	—	—
Coleoptera									
Carabidae	—	—	—	1	1	2	—	1	1
Chantariidae	—	—	—	—	—	—	1	—	1
Chrysomelidae	3	3	6	5	1	6	6	—	6
Staphilinidae	2	—	2	1	1	2	1	—	1
Curculionidae	4	7	11	1	4	5	1	—	1
Coccinellidae	—	1	1	—	1	1	—	—	—
Coleoptera larva	1	1	2	—	1	1	2	—	2
Coleoptera indet.	16	1	17	1	4	5	1	—	1
Neuroptera									
Chrysopidae larva	—	—	—	—	1	1	—	—	—
Lepidoptera									
Psychidae	—	—	—	—	1	1	—	—	—
Lepidoptera indet.	—	—	—	—	—	—	1	—	1
Microlepidoptera larva	—	—	—	—	3	3	1	—	1
Lepidoptera larva indet.	5	—	5	2	—	2	—	—	—
Diptera									
Culicidae	3	—	3	1	1	2	—	—	—
Syrphidae	—	—	—	—	1	1	—	—	—
Drosophilidae	—	—	—	1	—	1	—	—	—
Diptera indet.	18	—	18	2	1	3	—	—	—
Hymenoptera									
Formicidae	35	3	38	—	8	8	—	—	—
Hymenoptera indet.	12	5	17	—	7	7	—	—	—
Tenthredinidae larva	1	—	1	1	—	1	—	1	1
Pseudoscorpionidea	—	—	—	—	5	5	—	—	—
Opilionidea	—	—	—	3	4	7	—	—	—
Araneidea									
Agelenidae	—	—	—	—	—	—	1	—	1
Thomisidae	—	1	1	—	—	—	—	—	—
Salticidae	—	—	—	—	2	2	—	—	—
Araneidea indet.	8	1	9	3	10	13	2	—	2
Acaridea	12	—	12	—	—	—	—	—	—
Indet. Invertebrates	1	5	6	—	4	4	—	—	—
Plant food	5	7	12	—	4	4	—	—	—
Total	198	40	238	52	93	145	41	9	50

Frogs were collected in two characteristic habitats of the Kis-Balaton Nature Reserve in September, 1984. One of the study plots was along the bank of the River Zala (wet habitat). Vegetation consisted mainly of *Glyceria maxima* and *Phragmites communis* with a great diversity of *Carex* and weed species. The other plot was on a small island surrounded by a great swamp. *Alnus glutinosa* was the most frequent tree species on the island. In the shrub layer *Sambucus nigra*, *Urtica dioica*, *Solidago gigantea* and different *Carex* species were numerous.

Although several methods (emetics, faeces analysis) are known to get information on the food composition of anuran species (OPATRNY, 1980), stomach content analysis is the most reliable and frequently used method nowadays (GRIFFITHS, 1986; WHEATER, 1986; KÜHLHORN, 1960). Using this method the greatest error could be caused by the different digestibility of the food items. The differences in digestibility can change the relative proportion of prey groups eaten by frogs (HYSLOP, 1980; LEGLER and SULLIVAN, 1979; OPATRNY, 1980). All items found in the frog stomachs were totally intact. Even though the weakly chitinized caterpillars, aphids and small crustaceans were kept in perfect state.

Percentage similarity in the diet among the three frog species was computed using RENKONEN's (1938) similarity index.

## Results

### *Description of the Kis-Balaton collection*

The most numerous species was *R. esculenta* in both habitats. Altogether 239 food items were indentified in the stomach contents (Table 1). This species fed mainly on hymenopterans, namely ant species. Coleopterans and homopterans also formed a great part of the diet with the abundance of Curculionidae and *Cassida* as well as small Jassidae larvae. There was a great similarity between the diet of *R. esculenta* in the two habitats. In the wet habitat frogs preferred hymenopterans while in the dry habitat they ate more coleopterans. Besides coleopterans and hymenopterans *R. arvalis* usually fed on spiders and snails. Individuals living in the dry habitat preferred ants, spiders and millipeds comparing to those caught in the wet habitat. Vegetable food occurred occasionally in the stomach of all the three species. We found seeds of plants in the dry habitat in *R. esculenta* while few items of *Lemna* species occurred in the diet of *R. arvalis* in the wet habitat.

Only few individuals of the third species, *R. dalmatina*, were caught at the study plots. Although this species can be observed even in extremely dry habitats out of the spawning season we found the individuals mainly in the wet habitat. The most important food types of this species were beetles, isopods, snails and bugs.

### *Description of Szabó's collection*

158 individuals belonging to three *Rana* species were collected at different parts of Hungary during 6 years (Table 2). Identification cards of frogs are available in the Natural History Museum, Budapest. All the three species showed similar prey type preference to those we found in Kis-Balaton. The most abundant prey types were coleopterans, spiders, ants and dipterans. In SZABÓ's collection *R. esculenta* fed much more Collembola than the individuals caught in Kis-Balaton. This species also ate a lot of carabid and curculionid beetles as well as ants and dipterans. Almost fifty percent of the diet of *R. arvalis* consisted of beetles (mainly Carabidae species). Spiders were also found frequently in the diet. The proportion of caterpillars was higher in SZABÓ's collection than in our samples. *R. dalmatina*, which was usually collected in drier habitats comparing to the other two species, preferred spiders, beetles, diptera larvae and bugs.

Table 2. Food composition (based on prey items) of three anuran species in Szabó's collection. Data were collected from 1956 to 1961 at different parts of Hungary (sample size in parentheses)

Prey taxon	Anuran species		
	<i>R. esculenta</i> (55)	<i>R. arvalis</i> (45)	<i>R. dalmatina</i> (10)
<b>Mollusca</b>			
Ctenobranchiata			
<i>Bithynia leachi</i>	1	—	—
<i>Fagotia acicularis</i>	6	—	—
Basommatophora			
<i>Segmentina nitida</i>	1	—	—
<i>S. complanata</i>	1	—	—
<i>Radix ovata</i>	2	—	—
<i>R. sp.</i>	—	1	—
Stylommatophora			
<i>Succinea putris</i>	3	—	—
<i>S. oblonga</i>	1	—	—
<i>Cochlicopa lubrica</i>	—	1	—
<i>Vallonia pulchella</i>	—	1	—
<i>Zebrina detrita</i>	1	—	—
<i>Daudebardia fallax</i>	1	—	—
<i>Arion circumscriptus</i>	—	—	1
Limacidae	—	—	1
<i>Aegopinella nitens</i>	—	—	1
<i>Ae. sp.</i>	1	—	—
<i>Fruticicola fruticum</i>	—	2	—
<i>Monacha cartusiana</i>	8	5	2
<i>Perforatella incarnata</i>	—	—	1
<i>Trichia unidentata</i>	—	1	—
Pulmonata indet.	2	2	1
<b>Crustacea</b>			
Isopoda			
<i>Asellus aquaticus</i>	2	—	—
<i>Protracheoniscus amoenus</i>	—	—	3
<i>P. saxonicus</i>	—	—	2
<i>Trachelipus rathkii</i>	6	1	3
<i>Porcellio sp.</i>	—	—	1
<i>Ligidium hypnorum</i>	—	—	3
<i>Armadillidium spp.</i>	—	1	2
Diplopoda			
<i>Glomeris hexasticha</i>	—	—	1
<i>Polydesmus complanatus</i>	—	—	1
<i>Unciger foetidus</i>	1	—	—
Chilopoda			
<i>Lithobius muticus</i>	—	2	4
<i>Geophilus insculptus</i>	—	—	1
<b>Insecta</b>			
Collembola			
<i>Podura aquatica</i>	48	—	4
<i>Lepidocyrtus paradoxus</i>	—	1	—
<i>Isotomurus palustris</i>	8	—	1
<i>Orchesella cincta</i>	1	—	—
<i>Entomobrya spp.</i>	—	2	—
<i>Hypogastrura spp.</i>	39	—	—

Table 2./2

Prey taxon	Anuran species		
	<i>R. esculenta</i> (55)	<i>R. arvalis</i> (45)	<i>R. dalmatina</i> (10)
Odonata			
<i>Calopteryx virgo</i>	2	—	—
<i>Sympetrum vulgatum</i>	1	—	—
Libellulidae larva	—	1	3
Blattidea	—	—	3
Orthoptera			
<i>Tetrix subulata</i>	—	2	—
Acrididae	1	1	3
Tettigoniidae indet.	4	—	1
<i>Oecanthus pellucens</i>	—	—	1
<i>Gryllotalpa gryllotalpa</i>	2	—	—
Dermaptera			
<i>Chelidurella acanthopygia</i>	—	—	4
Heteroptera			
<i>Aethus nigratus</i>	1	—	—
<i>Eurygaster maura</i>	1	—	—
<i>Eurydema oleraceum</i>	1	—	—
<i>Palomena</i> sp.	1	1	1
<i>Aelia acuminata</i>	—	1	—
Miridae indet.	3	—	—
<i>Chaitophorus</i> sp.	—	—	5
<i>Ischnodemus sabuleti</i>	1	—	—
<i>Nabis</i> sp.	—	—	2
Naucoridae indet.	2	—	—
<i>Agramma</i> sp.	1	—	—
Heteroptera larva	1	—	—
Homoptera			
<i>Cixius</i> sp.	—	—	1
<i>Calligipona</i> sp.	—	—	2
<i>Tettigometra</i> sp.	1	—	—
Cicadidae indet.	—	—	1
<i>Centrotus cornutus</i>	—	1	1
<i>Tettigella viridis</i>	—	1	4
Jassidae indet.	1	—	2
<i>Aphidius</i> spp.	—	—	5
<i>Aphis</i> sp.	—	—	27
<i>Megaphthalmus</i> sp.	—	—	1
Neuroptera			
<i>Planipennis</i> sp. larva	1	—	—
Neuroptera indet.	—	—	1
Mecoptera			
<i>Panorpa communis</i>	—	—	1
Physopoda			
<i>Trips</i> sp.	—	1	—
Coleoptera			
<i>Dryops</i> sp.	2	—	—
<i>Haliplus</i> sp.	2	—	—
<i>Carabus nemoralis</i>	1	—	—
<i>C. granulatus</i>	—	2	—
<i>C.</i> spp.	3	2	2
<i>Clivina fassor</i>	—	1	—
<i>Stomis pumicatus</i>	—	1	—

Table 2./3

Prey taxon	Anuran species		
	<i>R. esculenta</i> (55)	<i>R. arvalis</i> (45)	<i>R. dalmatina</i> (10)
<i>Drypta dentata</i>	—	1	—
<i>Platambus maculatus</i>	1	—	—
<i>Bembidion</i> spp.	3	1	—
<i>Amara</i> spp.	1	6	1
<i>Harpalus</i> spp.	15	11	—
<i>Pterostichus</i> spp.	1	2	—
<i>Elaphrus</i> sp.	—	1	—
<i>Abax</i> sp.	1	1	—
<i>Agonium</i> sp.	—	1	—
<i>Dyschirius</i> spp.	1	1	—
<i>Liodes</i> sp.	—	—	1
<i>Laccophilus</i> sp.	1	—	—
<i>Rhantus</i> sp.	1	—	—
<i>Graphoderes</i> sp.	1	—	—
<i>Dytiscidae</i> indet.	1	—	—
<i>D.</i> indet. larva	—	—	1
<i>Anacaena globosa</i>	1	—	—
<i>Helophorus</i> spp.	4	—	1
<i>Phyllidrus</i> spp.	2	—	—
<i>Hydrophilidae</i> indeet.	1	—	—
<i>Silpha obscura</i>	1	1	—
<i>S. carinata</i>	—	1	—
<i>Oxytelus</i> spp.	2	1	2
<i>Stenus</i> sp.	1	—	—
<i>Staphylinus</i> spp.	1	3	1
<i>Philonthus</i> sp.	—	—	1
<i>Paederus</i> spp.	—	1	2
<i>Staphylinidae</i> indet.	—	—	1
<i>Hister 4-maculatus</i>	—	1	—
<i>Heterocerus</i> sp.	2	—	—
<i>Cantharis rustica</i>	—	2	—
<i>C.</i> spp.	1	5	2
<i>Limonijs pilosus</i>	—	2	—
<i>Agriotes lineatus</i>	3	10	1
<i>Elateridae</i> indet.	—	9	2
<i>Throscus</i> sp.	—	—	1
<i>Cytillus sericeus</i>	1	—	—
<i>Meligethes</i> sp.	1	—	—
<i>Corticaria</i> sp.	—	1	—
<i>Charopus concolor</i>	—	1	—
<i>Coccinella septempunctata</i>	1	—	—
<i>Prinus</i> sp.	—	—	2
<i>Epicometis hirta</i>	4	—	—
<i>Cylindronotus aeneus</i>	—	—	3
<i>Notoxus</i> sp.	1	—	—
<i>Trox hispidus</i>	1	—	—
<i>Odontaeus armiger</i>	—	1	—
<i>Onthophagus</i> sp.	—	1	—
<i>Aphodius</i> spp.	8	3	1
<i>A.</i> sp. larva	—	1	—
<i>Dorcadion pedestre</i>	2	—	—
<i>D. decipiens</i>	—	1	—
<i>Hydrothassa glabra</i>	4	—	—
<i>Anthribidae</i> indet.	—	1	—

Table 2./4

Prey taxon	Anuran species		
	<i>R. esculenta</i> (55)	<i>R. arvalis</i> (45)	<i>R. dalmatina</i> (10)
<i>Bruchus</i> sp.	1	—	—
<i>Alophus triguttatus</i>	—	—	1
<i>Sitona</i> spp.	4	2	3
<i>Polydrusus</i> sp.	—	—	1
<i>Centorhynchus</i> sp.	1	—	—
<i>Phytonomus</i> sp.	2	—	—
<i>Bagous</i> sp.	1	—	—
<i>Baris</i> sp.	1	—	—
Curculionidae indet.	3	2	1
<i>Apion flavipes</i>	—	—	1
<i>A. ebenicurn</i>	—	—	1
<i>A.</i> spp.	—	1	2
<i>Dapsa denticollis</i>	—	—	2
<i>Platynus assimile</i>	—	1	—
<i>P.</i> sp.	—	1	—
Coleoptera indet.	7	9	4
Coleoptera indet. larva	5	—	6
Lepidoptera			
Microlepidoptera indet. larva	—	3	3
Coleoptera indet. larva	5	—	6
Lepidoptera			
Microlepidoptera indet. larva	—	3	3
<i>Hepialus humuli</i>	1	—	—
<i>H. rylvinus</i>	1	—	—
<i>Hypogynna morio</i> larva	—	1	—
<i>Malacosoma neustrium</i>	1	1	—
<i>M. castrense</i> larva	1	—	—
<i>Cucullia</i> sp. larva	—	2	—
Geometridae indet. larva	—	7	4
<i>Apatele rumicis</i> larva	—	1	—
<i>Tholera decimalis</i>	—	1	—
Noctuidae indet.	1	2	12
<i>Syntomis pbegea</i>	1	—	—
Hesperiidae indet.	1	—	—
Lepidoptera indet. larva	—	2	5
Diptera			
Chironomidae	4	—	1
<i>C.</i> larva	5	—	2
Culicidae larva	8	—	—
Tipulidae	—	—	2
Dolichopodidae	3	—	—
Ceratopogonidae	3	—	—
Emphididae	4	—	—
Syrphidae	1	—	1
Sciaridae	4	—	1
Asilidae	2	—	—
Bombyliidae	1	—	—
Ephyridae	1	—	—
Sciomyzidae	—	1	—
Borboridae	—	—	4
Phoridae	—	—	2
Mycetophilidae	—	—	1
Lonchopteridae	—	—	1

Table 2./5

Prey taxon	Anuran species		
	<i>R. esculenta</i> (55)	<i>R. arvalis</i> (45)	<i>R. dalmatina</i> (10)
Tachinidae	2	—	2
<i>Ravinia striata</i>	1	—	—
Diptera indet	3	—	4
Diptera indet. larva	6	—	18
Hymenoptera			
Tenthredinidae larva	—	1	1
Ophioninae	1	—	—
<i>Ephedrus</i> sp.	—	1	—
<i>Lagynodes pallidus</i>	1	—	—
Chalcididae	1	—	1
Cryptinae spp.	—	1	1
Proctotrupidae	—	—	1
Bethylidae	1	—	—
<i>Lasius</i> spp.	7	1	—
<i>Formica</i> spp.	3	3	1
<i>Myrmica ruginodis</i>	1	—	—
<i>M. scabrinodis</i>	1	—	—
<i>M.</i> spp.	10	—	—
<i>Tetramorium</i> spp.	14	—	—
<i>Halictus</i> sp.	1	—	—
Hymenoptera indet.	2	1	1
Hymenoptera larva indet.	—	—	3
Opilionea			
<i>Platibunus triangularis</i>	—	—	2
<i>Liobunus</i> sp.	—	1	—
<i>Zacheus</i> spp.	—	—	5
Araneidea			
<i>Drassodes</i> sp.	—	—	1
<i>Robertus</i> sp.	1	—	—
Micryphantidae	—	1	—
<i>Oedothorax retusa</i>	1	—	1
<i>Leptyphantes</i> sp.	1	—	—
<i>Cercidia prominens</i>	—	—	1
<i>Araneus cornutus</i>	—	2	1
<i>Meta</i> sp.	2	—	—
<i>Tetragnatha</i> sp.	1	—	—
<i>Pachygnatha clercki</i>	1	3	1
<i>P. degeeri</i>	—	5	1
<i>Xysticus kochi</i>	—	3	3
<i>X.</i> spp.	1	1	1
<i>Oxyptila horticola</i>	—	1	1
<i>O. simplex</i>	—	—	1
<i>Thanatus striatus</i>	—	1	—
<i>Zora nemoralis</i>	—	—	2
<i>Clubiona caerulea</i>	—	1	—
<i>C. compta</i>	—	1	—
<i>C. lutescens</i>	—	1	1
<i>C.</i> spp.	4	2	7
<i>Micrommata virescens</i>	—	—	1
<i>Agroeca brunnea</i>	—	2	—
<i>Coelotes inermis</i>	—	—	3
<i>Cicurina cicur</i>	—	—	1
<i>Antistea elegans</i>	1	—	1



Table 2./6

Prey taxon	Anuran species		
	<i>R. esculenta</i> (55)	<i>R. arvalis</i> (45)	<i>R. dalmatina</i> (10)
<i>Tegenaria</i> sp.	—	1	—
<i>Pardosa saccata</i>	1	—	5
<i>P. lugubris</i>	—	—	1
<i>P. agrestis</i>	—	4	—
<i>P. spp.</i>	1	7	3
<i>Alopecosa tabalis</i>	—	—	1
<i>Trochosa terricola</i>	3	2	1
<i>T. ruricola</i>	—	1	3
<i>T. spp.</i>	2	1	2
<i>Pirata hygrophilus</i>	—	2	—
Acarina			
<i>Xenillus clypeator</i>	—	—	1
<i>Eugamasus lunulatus</i>	1	—	1
<i>Scheloribates laevigatus</i>	—	—	1
<i>Punctoribates punctum</i>	1	—	—
<i>Damaeus gracilipes</i>	1	—	—
<i>Zercon</i> sp.	3	—	—
Acarina indet. larva	2	—	—
Trombidiidae	—	—	1
Total	387	196	277

Between-species similarity was almost the same in the two collections (Table 3). The diet of *R. esculenta* and *R. arvalis* overlapped almost to the same extent in the dry and wet habitats.

Table 3. Food composition similarities (analysed on prey number) among three anuran species at two study plots of Kis-Balaton and in Szabó's collection

Species pair	Kis-Balaton			Szabó's collection
	Wet	Dry	Total	
<i>R. esculenta</i> — <i>R. arvalis</i>	.55	.52	.68	.53
<i>R. esculenta</i> — <i>R. dalmatina</i>	.48	—	.49	.51
<i>R. arvalis</i> — <i>R. dalmatina</i>	.58	—	.48	.56

## Discussion

In Hungary only few papers were published on the food composition of anuran species. RAINISS (1967) analysed the diet of *R. esculenta* in artificial fish ponds. The results were not surprising, frogs frequently ate small fish. In Kis-Balaton we did not find fish species in the frogs food. Four other papers described the diet of these *Rana* species from different parts of Europe. TYLER (1958) and KÜHLHORN (1960) found that *R. esculenta* feeds on Coleoptera, Hemiptera, Hymenoptera, Diptera, spiders, snails and Aphididae, while ZIMKA (1974) and LOMAN (1979) studied the diet of *R. arvalis*, which showed similar food type preference (Coleoptera, Hemiptera, Diptera, Aphididae, snails) to that found in *R. esculenta*. Similar food preference was found for *R. esculenta* and *R. arvalis* in this study.

Our results showed that all the three *Rana* species are generalist feeders. There were only small differences in the food composition of the species between dry and wet habitats. Based on the food items frogs usually foraged on the ground and on small plant species. Aquatic prey occurred accidentally in the diet. During their opportunistic feeding frogs usually apply mixed foraging strategies involving both sit-and-wait and widely-foraging methods. The low energy requirement of this foraging type allows frogs to catch every prey item which is ranged in their preferred size spectrum.

Usually there is a great similarity in the diet compositions of species in anuran communities (GRIFFITHS, 1986). This was found for the three *Rana* species in our study. Probably not the food type but the foraging site preference or the food size (if there is a remarkable difference in size between the species) can segregate frog species. The segregation along the prey size spectrum is probably more important within-population between the different sized age groups (FRASER, 1976; LOMAN, 1979; NUUTINEN and RANTA, 1986).

\*

This study was supported by the Hungarian Academy of Sciences and the Ministry for Nature Conservation. We thank G. GERE and S. ANDRIKOVICS for comments of an early version of this paper and É. LUDVIG for improving the English text. As frogs are under protection in Hungary, the permission to collect them was released by the Ministry for Nature Conservation. We are also indebted to M. SASS, P. LÓW, E. FUTÓ, I. LAZÁR and J. KOVÁCS for their help in the field. Dr. I. SZABÓ kindly allowed us to publish his data.

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